1. VEGETATION SUCCESSION: PAST AND PRESENT PERCEPTIONS

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INTRODUCTION

The aim of this paper is to introduce the notion of succession, summarizing its history, present state and intellectual trappings. I shall confine my remarks to vegetation, where the concept has its origin, and ignore planktonic, sea-bed and littoral successions, and also successions of heterotrophic organisms. These latter mostly have little in common with vegetation succession, and seem to have generated fewer intellectual lathers in their savants.

Although the concept of succession is both simple and useful, succession as a class of phenomena seen in the field is, like Medawar's (1969) description of biology, 'complex, messy and richly various'. It is thus perhaps not surprising that the literature about the idea reflects the confusion of the subject matter. I cannot better summarize the disorder enmeshing the concept than by quoting the opening remarks from the most comprehensive and thoughtful review of succession (McIntosh 1980) that I know: 'Succession is one of the oldest, most basic, yet still in some ways, most confounded of ecological concepts. Since its formalization ... in the early 1900s, thousands of descriptions of, commentaries about and interpretations of succession have been published and extended inconclusive controversy has been generated. Withal, no effective synthesis of the divergent observations from many different ecosystems, terrestrial and aquatic, has produced a body of laws and theories which ecologists, generally, have embraced. Repeated symposia on succession and the corollary problems of the succession concept, ... have not produced notable convergence of thought. Problems of conceptualization and terminology are still evident after three quarters of a century.'

The confusion in the literature, and the absence of an acceptable unifying theory, seem to spring largely from an unachievable search for an ecological Shangri-La. Even passing acquaintance with the subject matter shows that vegetation change in time stems from many different causes. Yet all these changes have at some time or other been termed succession. It should surprise no-one that changes from disparate causes cannot

be explained in a common way. A further reason for the unattainability of a unifying theory of succession derives from the individualistic nature of vegetation, first argued so clearly by Gleason (1917, 1926) over 60 years ago. These matters have been common knowledge for so long that I can only conclude that the compulsive search by so many workers this century for a universal generalization of succession, a search that appears still to be in progress (Finegan 1984), arises from emotion rather than logic.

The phenomena of succession are too numerous to review here, while the phenomenon of the study of succession was recently reviewed in detail by McIntosh (1980, 1981). Therefore, in addition to discussing the development of the concept of succession, I shall develop the argument that it is pointless to pursue the quest for the ecological grail of a single universal generalization of succession that will be both useful and widely accepted. Finally, I shall outline my particular approach to using knowledge of succession in land management.

HISTORICAL AWARENESS OF SUCCESSION

'Succession' implies a sequence of something in time or place. In the ecological literature it has mostly been used to denote sequences of change in time. The first to use the term in this sense may have been De Luc (1806, cited by Clements 1916) in his description of hydroseres in northern Germany. However, an awareness that vegetation tends to change with time, and particularly that change follows disturbance, must be far older. The effects of forest and prairie fires caused by lightning, and of other gross disturbances, will have been seen by the earliest specimens of *Homo sapiens*, and seen more frequently by those still remote, hunter-gatherer ancestors who first chanced upon the use of fire for driving game or clearing forest. The early practitioners of slash-and-burn cultivation will have seen the successions they caused. They were active in Britain in the postglacial Atlantic period for certain (Dimbleby 1962; Romans & Robertson 1975), and possibly in the Boreal (Smith 1970), and active in Mediterranean regions even earlier (Naveh & Dan 1973).

In classical times, Theophrastus (*c.* 300 BC) wrote about vegetation changing with time (Hort 1916), and several early Roman writers were aware of succession (Spurr 1952). Clements (1916) reviewed the post-renaissance literature, and traced observations on successions back to 1685. The tendency for individuals of particular tree species to be replaced after death by those of different species was remarked on early. Cochon (1846) claimed the phenomenon was first recognized by Telles

d'Acosta in the eighteenth century. However, the most remarkable early study comprised the felling experiments of Dureau de la Malle (1825), an inquisitive and observant Normandy landowner, who concluded: '... the alternative succession in the reproduction of plant species, especially when they are forced to live socially, is a general law of nature, a condition essential to their conservation, to their development. This rule applies equally to long-lived, high forest trees, to shrubs and undershrubs, controls the vegetation of social plants, of artificial and natural grasslands, of perennial, biennial and annual species, living socially or even isolated'. Awareness of change, and of one cause, competition, is shown by De Candolle's remark in 1820 (cited by Warming & Vahl 1909) that: 'All the plants of a country, all those of a given place, are in a state of war, the ones relative to the others.'

DEVELOPMENT OF THE CONCEPT

From the mid-nineteenth century, successions were noted increasingly in the literature. While foresters in North America at least seemed to assume that forest succession was a general phenomenon (Dawson 1847; Thoreau 1860; Douglas 1875, 1889), the published views of botanists studying vegetation and plant geography developed more slowly. Braun-Blanquet (1932) claimed that Kerner (1863) was 'the real founder of the doctrine of the development of communities', from his studies in the Danube Basin. Clements (1916) ignored Kerner in his historical review, but cited Hult's 1885 publication on the vegetation of Blekinge in Finland as evidence that Hult was 'the first to fully recognize the fundamental importance of development in vegetation'. Hult argued that the distribution of different kinds of vegetation could only be understood with knowledge of their development. However, Warming (1895) seems to have been the first to stress that vegetation change was universal and unceasing.

Warming did not elaborate his ideas further, and the concept of succession was only developed in detail at the turn of the century in North America by Cowles and Clements, at first apparently independently. Cowles, a physical geographer, studied the dynamics of sand dunes at the head of Lake Michigan (Cowles 1899, 1901), and found that although the dunes were formed and destroyed by wind, their development between formation and destruction was largely controlled by their vegetation. From these and other studies, Gleason argued that vegetation in general will change as the physiography changes, though he also noted that vegetation can often change faster than geomorphology. Cowles' (1911)

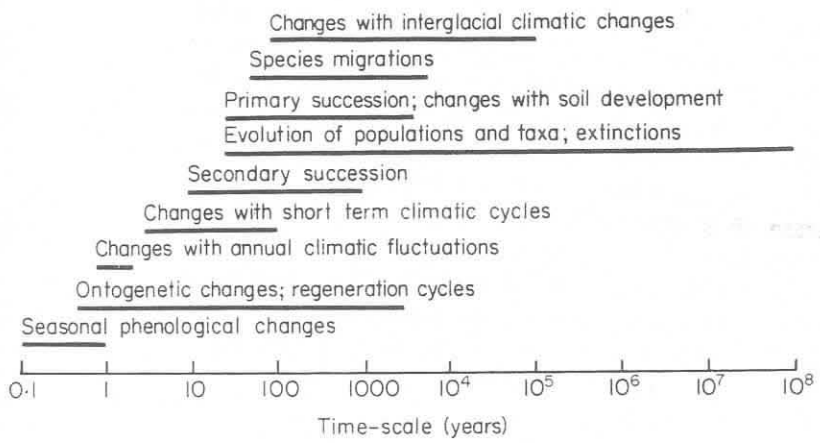

FIG. 1.1. Time-scales of vegetation change from different causes.

conclusions were soundly based on observation, and bear restating. On succession, Cowles wrote, 'the original plant formations in any habitat give way in a somewhat definite fashion to those that come after.' Cowles also recognized that changes in vegetation caused by climatic, topographic and biotic changes occurred at different rates and concurrently, 'this complex of cycle within cycle, each moving independently of the others and at times in different directions', a point that is still too infrequently stressed. Fig. 1.1 shows the relative time-scales of various kinds of vegetation change.

Concurrently with Cowles, Clements began to study the Nebraska prairies. In 1898, Pound and Clements wrote, 'formations and subordinate groups are in stable equilibrium only rarely and usually for a comparatively short time'. Shortly after, Clements (1904) published an excellent empirical and analytical account of the causes of succession, in which he clearly distinguished between primary succession on newly exposed surfaces which had never borne vegetation before, and secondary succession where vegetation on soils already developed had been damaged or destroyed. In 1916, however, Clements published the monumental work on succession by which he is most commonly remembered. This is a mix of scholarship and sound observation curiously blended with a purely deductive and hypothetical classification of succession based on the concept of 'climax' vegetation, an attempt to create a unifying theoretical framework of succession. His speculative theory was fatally flawed from the outset, and has been criticized often and in detail (Gleason 1917, 1926, 1927, 1937; Colinvaux 1973; Drury & Nisbet 1973;

Miles 1979). Yet his influence on the development of plant ecology in America and Britain was profound. Gleason (1975), Clements' contemporary, explained his motives thus: 'He was a classicist, and Latin and Greek are precise languages, with an elaborate system of conjugations and declensions. Perhaps this led him to attempt an equally precise and elaborate classification of the whole content of ecology'. Egler (1951) explained the phenomenon in similar vein: 'We have Clements the uncompromising idealist, the speculative philosopher, driven by some demon to set up a meticulously orderly system of nature, as neatly organized and arranged as the components of Dante's Inferno.'

Why did Clements' theory command such support? Doubtless one reason is the human yearning for order, to discern patterns in apparent chaos, to transform collections of facts into predictive theory. Parts of Clements' schema fitted with prevailing sentiment at the time. The 'organismic concept' was a widely accepted tradition in natural history years before Clements took it in hand (McIntosh 1980). His views on the persistence of climax vegetation, and on the convergence of successions to the regional climax, fitted with the then current geomorphological theory of Davis (1909), and with the lack of present knowledge on climatic variability in time. Perhaps above all it was his prestige as a practical man in the field that won him support. Egler (1951) wrote: 'We have Clements the practical realist, the Clements who impressed the soil conservationists, agronomists and range managers with his down-to-earth understanding of land management, the Clements who could discuss and write convincingly about such problems with almost complete absence of technical terminology and intellectual gyrations. . . . It is easy to see how Clements gained the respect and enthusiasm of the practical field man, who would then "accept" the complicated philosophy, not as something which he really comprehended, but as something which must be "right" since it came from Clements the realist.'

The ideas in Clements' (1916) work proved seminal, though perhaps less for their intrinsic merit than for the opposing ideas they created, which might not otherwise have been developed and presented so clearly! However, as Watt (1964) noted, Clements was largely responsible for injecting a dynamic principle into a largely static ecology.

VARYING INTERPRETATIONS OF SUCCESSIONAL PHENOMENA

What is succession? Recent definitions have tended to be broad, to exclude only seasonal, fluctuational and cyclic changes from the gamut of

recognized vegetation changes, and to be mutually consistent: 'a progressive alteration in the structure and species composition of the vegetation' (Grime 1979); 'directional change away from an initial state. ... changes which markedly alter the appearance of a patch [of vegetation] such that it can be considered to have changed into a different type' (Miles 1979); 'the directional change with time of the species composition and vegetation physiognomy of a single site' (Finegan 1984). Succession thus hinges on the occurrence of gross, directional changes in species composition. Such changes may occur when species die and are replaced by others, but, in secondary succession and the later stages of primary succession, may just reflect changing patterns of dominance by species present through most or all of the succession period as propagules. This latter can be represented schematically as:

$$A_{BCD} \rightarrow {}_{A}B_{CD} \rightarrow {}_{AB}C_{D} \rightarrow {}_{ABC}D$$

This definition is broader than that adopted by Clements, but narrower than Gleason's. Clements (1916) defined succession as 'a sequence of plant communities marked by the change from lower to higher life-forms.' He also held that reverse successions, from higher to lower life-forms, were impossible. 'Succession is inherently and inevitably progressive. ... Regression, an actual development backwards, is just as impossible for a sere as it is for a plant.' Many instances have now been published in which environmental variability has caused just that; for example, fluctuating ecotones between forest and prairie, fluctuating montane treelines, northern forests turning into bogs (Drury 1956; Ugolini & Mann 1979). Gleason (1953, 1975) recorded finding one reverse succession which seems to have been a milestone in the development of his ideas: 'I found a pond developing on top of a sand dune, not a stone's throw from the side of the dune and 30 feet or so above the adjoining land. It started in a blow-out, waterproofed its own bottom with blue-green algae and the remains of Polytrichum, and then these zones of hydrophytes marched steadily up the hill. Hydrophytes moving centrifugally! Impossible. Unheard of.' (Gleason 1975).

Gleason's (1927) definition of succession was very broad: 'The successional phenomena of vegetation include all types of change in time, whether they are merely fluctuating or produce a fundamental change in the association.' Because succession has traditionally been used to describe vegetation change at a site level, Gleason's definition seems unnecessarily broad. Although the distinctions are sometimes arbitrary, fluctuations and regeneration (which is cyclic) can commonly and usefully be distinguished from directional change, i.e. succession (Miles 1979).

That being so, it is sensible to use the definition of succession with the greater information content.

Does succession have any fixed attributes, other than the defined floristic change? Drury & Nisbet (1973) argued not, and I agree (Miles 1979). However, attempts have been made to define succession in terms of functional attributes of ecosystems, notably by Margalef (1958, 1963, 1968) and Odum (1969). I find these interesting, but not giving useful insights in terms of plants or vegetation. Thus, Margalef (1958) wrote: '... succession may be defined as a gradual, irreversible change in the structure of a mixed population in the direction of a replacement of systems slightly structured and having a rapid dynamics, made up of relatively small organisms, having a high productivity/biomass relationship, adapted to the rapid utilization of the resources of the medium, by other, more stable, communities made up of larger organisms with a greater thermodynamic output, adapted to an efficient utilization of the resources and having a lower productivity/biomass relationship.' This is just what Clements said, that succession is a sequence from lower to higher life-forms! The rest follows automatically from the differing biology of varying life-forms. Later in the same paper, Margalef gave a terser definition: 'In thermodynamics, succession can be described as the acquisition of greater efficiency in exploiting the medium and reducing to the minimum the dissipation of energy.' Then in 1968 he wrote: '... succession ... appears to be a process of self-organization occurring in every cybernetic system with the properties of an ecosystem. ... The process of succession is equivalent to a process of accumulating information.' The briefest 'systems' definition I have encountered is Noble's (1981) statement, 'Succession is the time-dependent integration of all ecological processes at a site.' Such definitions may give insights to a systems expert, though Margalef's stress on the irreversibility of succession will certainly mislead, but I see no relevance to a vegetation manager.

However, vegetation or ecosystem properties are of great interest to most vegetation managers, particularly yields of timber and other crops. Fig. 1.2 shows the general pattern of net ecosystem production (NEP) during secondary succession. Initially after disturbance, organic matter decomposition exceeds production, so NEP has negative values. Closely correlated with NEP are element output rates. Most elements are lost in surface run-off and drainage waters. Any sudden increase in output rates after disturbance to vegetation (because uptake by the vegetation is greatly reduced) are of potential concern to water and fisheries boards.

There are other interesting ways of looking at vegetation during succes-

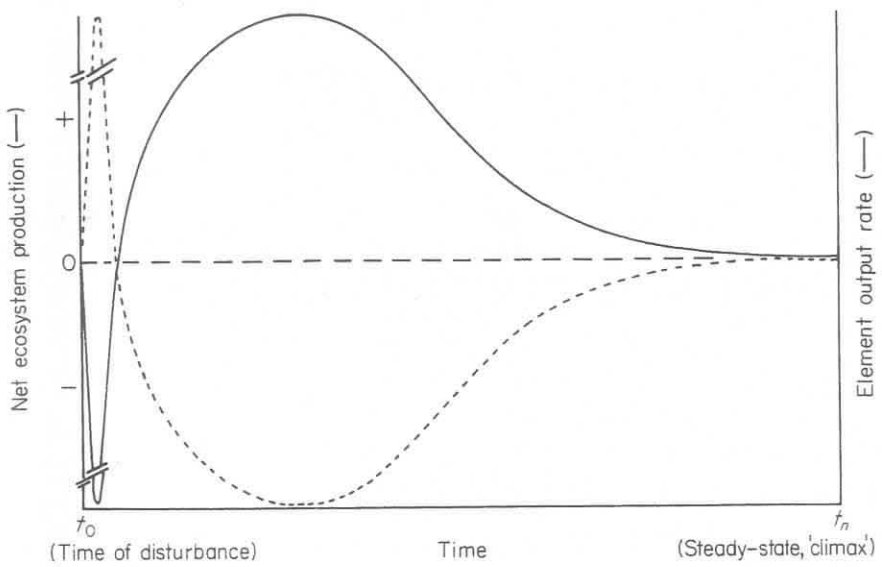

FIG. 1.2. Patterns of change in net ecosystem production and element output rate (assuming constant input rates) during secondary succession. (After Gorham, Vitousek & Reiners, 1979.)

sion. Grime (1977, 1979 and this volume) has argued that evolution in plants has produced three main 'strategies' in response to competition, stress and disturbance, and that knowing the potential productivity of a site makes it possible to recognize the probable sequence of life-forms there during succession.

Regardless of plant strategies, an important determinant of the course of any succession, and the prime determinant of secondary succession, is the range of species present at the outset and migrating to the site early in succession. The proximity of seed sources is thus important (Kellman 1970; Miles 1979). Lepart & Escarré (1983) have shown how the relative importance of different plant dispersal mechanisms varies with time during succession of abandoned fields around Montpellier in southern France (Fig. 1.3). As expected, most early colonizers were wind-dispersed, but after about 10 years there was an increase in the proportion of species dispersed via faeces, and of species with large seeds or fruits without regular dispersal mechanisms other than gravity or chance dispersal by animals (e.g. *Quercus coccifera* acorns).

Clements (1916) recognized the importance of species accessibility, especially in secondary succession, where a productive soil had already

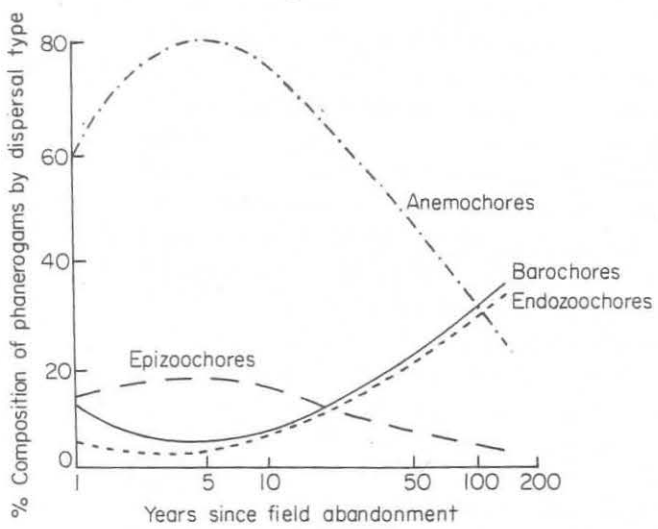

FIG. 1.3. Relative frequency of four methods of propagule dispersal in the phanerogam flora of abandoned fields around Montpellier, southern France, at different times after abandonment. (After Lepart & Escarre 1983.)

developed, and did not necessarily expect site modification to be important in secondary succession, nor progressive colonization by species: 'Secondary bare areas . . . normally possess viable germules of more than one stage, often in large number, retain more or less of the proceeding reactions, and consequently give rise to relatively short and simple seres. . . . In some cases it seems that the seeds and fruits for the dominants of all stages, including the climax, are present at the time of initiation.' Clements thus stressed the importance in secondary succession of the species composition at the time of disturbance, an idea usually attributed to Egler (1954).

One particularly interesting approach is to analyse which properties of species determine their successful reproduction and survival following disturbance. Gill (1975) and Naveh (1975) listed attributes that help species to survive recurrent fires. Noble & Slatyer (1977, 1979, 1980) termed such properties 'vital attributes', showed how these could be used to predict a qualitative replacement sequence during regeneration after fire, and point out the major changes (again qualitatively) in dominance and composition. They showed that the scheme worked for several different vegetation types, while Hobbs, Mallik & Gimingham (1984) recently showed that the scheme also depicted the sequence of relative abundance

in *Calluna vulgaris* dominated heathland in north-east Scotland. Noble and Slatyer's classification is a clever formalization of species properties that ecologists have long used in an unsystematic way in predicting succession on the basis of experience. Its two major disadvantages are that it does not allow quantitative predictions, and is effectively dependent on a vegetation type in which all species occurring in the succession are present at the outset in some life-stage or other, establish together if not already established, and subsequently co-exist. Unlike Grime's (1977, 1979) model, there is no way of indicating if a particular species, arriving at the site some years after the disturbance, can compete effectively and establish. Nor does the scheme allow for the implications of site modification. It has been tested on the special case of vegetation adapted to recurrent fire. The process of canopy redevelopment of such vegetation after fire is probably best thought of as 'regeneration' or 'cyclic change' (Miles 1979), rather than succession. It is thus somewhat misleading to suggest the scheme at its present state of development can be used to predict successional change (see Noble & Slatyer's (1980) and Noble's (1981) titles). The scheme can however be used to examine multiple pathways of post-fire regeneration (Cattelino *et al.* 1979).

Clements' concept of succession included three major points apart from directionality and irreversibility: succession proceeded (i) deterministically (because it always went in the same direction to the same climax), (ii) to climax vegetation (i.e. the end-point of succession), and (iii) was driven by reaction (i.e. the effects that the plants had on their environment, now commonly termed site modification). The determinism arose from Clements' (1916) extreme views on the nature of vegetation: 'The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity. As an organism the formation arises, grows, matures, and dies. ... each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development.' Braun-Blanquet (1932) called this view 'a flight of imagination', while Gleason (1917) published an immediate and cogent rebuttal, later repeated and amplified (Gleason 1926, 1937). However, the 'organismic concept' survives, barely disguised, in the 'systems approach' of the computer age (Margalef 1963, 1968; Odum 1969; Whittaker & Woodwell 1972, Patten 1975), an age when 'the things that count are those that can be counted' (Egler 1970).

What is climax vegetation? Clements (1916) defined it as follows: 'Every complete sere ends in a climax. This point is reached when the occupation and reaction of a dominant are such as to exclude the invasion of another dominant.' However, he did not regard climax as unchanging:

'No climax area lacks frequent evidence of succession, and the greater number present it in bewildering abundance. . . . the most stable association is never in complete equilibrium, nor is it free from disturbed areas in which secondary succession is evident.' Later, in the context of his assumption that a climax formation was an organism, he wrote, 'succession is reproduction'. Cowles (1901) regarded climax as something rather less tangible: 'The condition of equilibrium is never reached, and when we say there is an approach to the mesophytic forest, we speak only roughly and approximately. As a matter of fact we have a variable approaching a variable rather than a constant.' Cooper (1926) stated forthrightly that the concept of the climax was, 'more or less subjective and artificially imposed upon the facts of nature', although he added that it was exceedingly useful.

Yet like succession, the climax concept, which is simple enough on a site basis, has caused a deal of pother and heart searching (Whittaker 1951, 1953). Over 70 years ago Harper (1914) noted that every different soil type seemed to have its own characteristic successional and climax vegetation. Further, acceptance of Gleason's ideas about the nature of vegetation must lead to rejection of any notion of a widespread climatic climax. Fifty years ago Braun-Blanquet (1932) suggested that Clements had overemphasized the concept of climax, because 'the areas today occupied by climax stages have become greatly reduced, and sometimes have become almost completely obliterated.' With this even truer today, and with increasing knowledge that long-term stability in vegetation is the exception rather than the rule, the concept approaches irrelevance. Certainly the term seems out of favour, except where, as in range management (Meeker & Merkel 1984), it still has practical utility.

How important is reaction as a driving force in succession? We should remember that Clements (1916) mostly referred to primary succession, i.e. succession on new, previously unvegetated bare areas such as lakes, rocks, fresh sand dunes, lava flows, moraines or mine and quarry waste, all initially sterile, and all with undifferentiated and usually unweathered soils. In all such cases, a degree of site modification is essential for succession to proceed. At the least, lakes must fill with sediment, and soils must accumulate the level of nitrogen capital needed to sustain non nitrogen-fixing plants (Bradshaw *et al.* 1982); plant growth on site is usually important in bringing about these changes. It is in secondary succession that the extent to which reaction can act as a driving force is uncertain. Many soil properties inevitably change during secondary succession (Miles 1981a, 1985b), perhaps pH and rates of nutrient cycling in particular, but there is little substantive evidence that they materially

influence the sequence of species changes. The best documented example may be when *Betula pendula* and *B. pubescens* colonize *Calluna*-dominated moorland (Miles & Young 1980; Miles 1985a). Gross changes can then occur in soil chemical and structural properties which permit many plant species to colonize the field layer that cannot grow in the moorland soil.

SUCCESSIONAL PATHWAYS

Multiple pathways

Patterns of vegetation change in time show a bewildering variety. Cooper (1926), a student of Cowles, implied this in his analogy: '... the vegetation of the earth presents itself as a flowing stream, undergoing constant change. It is not a simple stream but a "braided" one, of enormous complexity, with its origin in the far distant past. Its more or less separate and definite elements branch, interweave, anastomose, disappear, reappear. ... Vegetation as we see it today is thus a mere cross section of this complex stream.' A year later, Gleason (1927) wrote, more definitely: '... succession is an extraordinarily mobile phenomenon, whose processes are not to be stated as fixed laws, but only as general principles of exceedingly broad nature, and whose results need not and frequently do not ensue in any definitely predictable way.'

For all these remarks, it seems to have taken Walker's (1970) now classic synthesis of palynological studies of post-glacial hydroseres, which showed that 'variety is the keynote of hydroseral succession', for the notion of multiple pathways of succession to gain even limited acceptance. Now people are analysing successional data in ways that can detect multiple directions of change, and are finding them. Londo (1974) found a complex network of successional transitions from mapping 10 ha of dune slack vegetation successively in 1956, 1963 and 1968. Fig. 1.4 gives a simplified graphic account. Most of the vegetation units showed retrogressive trends to some extent. The most important unit that did not was *Hippophaë* scrub, but it is probable that insufficient time had passed for this either to degenerate with stand senescence, or to be succeeded by a different woody species. Dorp *et al.* (1985) found similar complex successional networks on a larger area of dunes, and Hogeweg (cited by Maarel & Werger, 1978) found them on saltmarsh. All three instances, and Walker's (1970) study, were of primary successions, but secondary successions behave similarly. Abrams, Sprugal & Dickmann (1985) found several directions of change during natural regeneration of burnt and felled

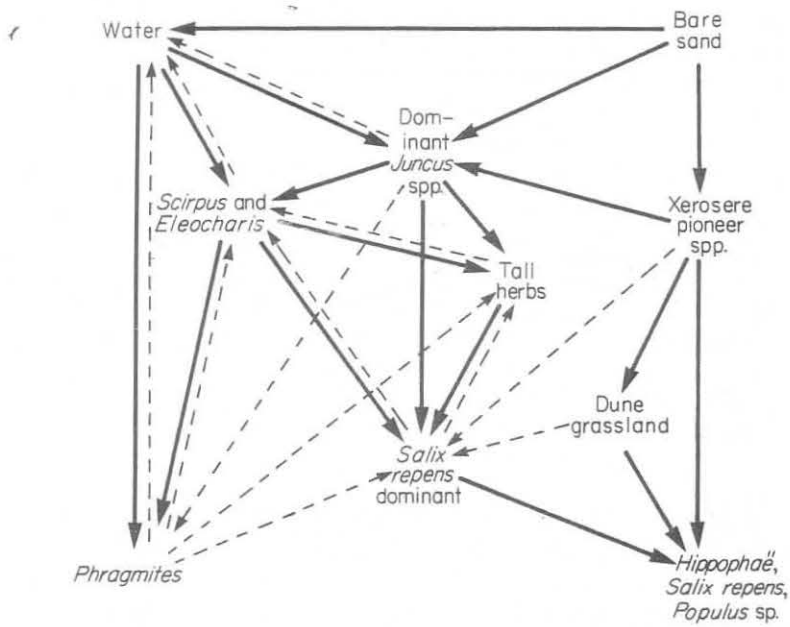

FIG. 1.4. Simplified successional trends during 1956–68 in dune slacks near Haarlem, the Netherlands. Solid lines represent major trends, dashed lines, minor trends. (From Londo 1974, courtesy of Dr W. Junk Publishers.)

stands of *Pinus banksiana*. Bakker *et al.* (1983) found multiple transitions when they subjected 11 ha of heathland, woodland and pasture to sheep grazing, at a mean stocking rate of 3 sheep ha^{-1} $year^{-1}$, during 1972–77. Table 1.1 gives the transition probabilities among four aggregate vegetation units from heathland only. Only the grassland dominated by *Molinia caerulea* did not show appreciable change to at least one other type.

Successional sequences and mechanisms

There has been considerable recent interest in mechanisms of succession. Egler (1954) stimulated the interest, Horn (1976) and Whittaker & Levin (1977) suggested examples, but Connel & Slatyer's (1977) paper, devoted largely to suggested mechanisms, caught the ecological community's imagination, and its terminology is now widely used. Fig. 1.5 indicates the replacement sequences suggested for succession by these authors. Fig. 1.5a is the 'model' implied by Clements (1916) and explicitly stated by other workers for primary succession. To my knowledge, no-one has ever

TABLE 1.1. Transition probabilities among four aggregated vegetation units* in 3 ha of grassy heathland during 1972–77 (from Bakker *et al.* 1983)

		Vegetation in 1972			
		1	2	3	4
Vegetation in 1977	1	0·36	0·04	0	0·01
	2	0·26	0·39	0·04	0·01
	3	0·16	0·57	0·68	0
	4	0·22	0	0·28	0·98

* Type 1, *Calluna vulgaris* and *Erica tetralix* predominant, with >50% cover; type 2, *Calluna* and *E. tetralix* predominant, with 20–50% cover; type 3, *Molinia caerulea* predominant, with >50% cover; type 4, grassland with <50% cover of *Molinia*.

shown that this pattern of successive waves of colonizing species ever occurs in secondary succession. 'Direct' succession (Fig. 1.5b) occurs in tundra and desert vegetation, where succession can be just the direct recolonization by the earlier occupants because no 'successional' species grow there (Shreve 1942; Muller 1952; Babb & Bliss 1974).

The model in Fig. 1.5c is that described by Egler (1954) for succession in abandoned fields, a sequence that was also implied by Clements (1916) for secondary succession. Egler noted that there was a tendency for most species seen during succession either to be present at the outset, as buried seed, rhizomes or other perennating organs, or to colonize within a few years. Many studies have now shown that the initial floristic composition is an important factor. In areas regenerating after fire, it seems usually to be the predominant factor, which is why Noble & Slatyer's (1977, 1979, 1980) system of 'vital attributes' can predict the regeneration sequence. Fig. 1.6 gives an example, the generalized sequence, averaged from a large number of sites, of vegetation change after burning *Calluna*-dominated moorland in part of north-east Scotland. Of the major components, only the pleurocarpous mosses were not recorded in the first year after burning. This model does not clearly differ from that in Fig. 1.5d, though Egler (1954) and others have suggested that distinct phases of dominance occur because of differences in the growth rates of different groups of plants, typically in the sequence: annual herbs, perennial herbs, short-lived woody plants, long-lived woody plants.

The model in Fig. 1.5d seems to occur commonly during old-field succession when species characteristic of later phases of the sequence are not present at the outset, but invade during the succession. Because they

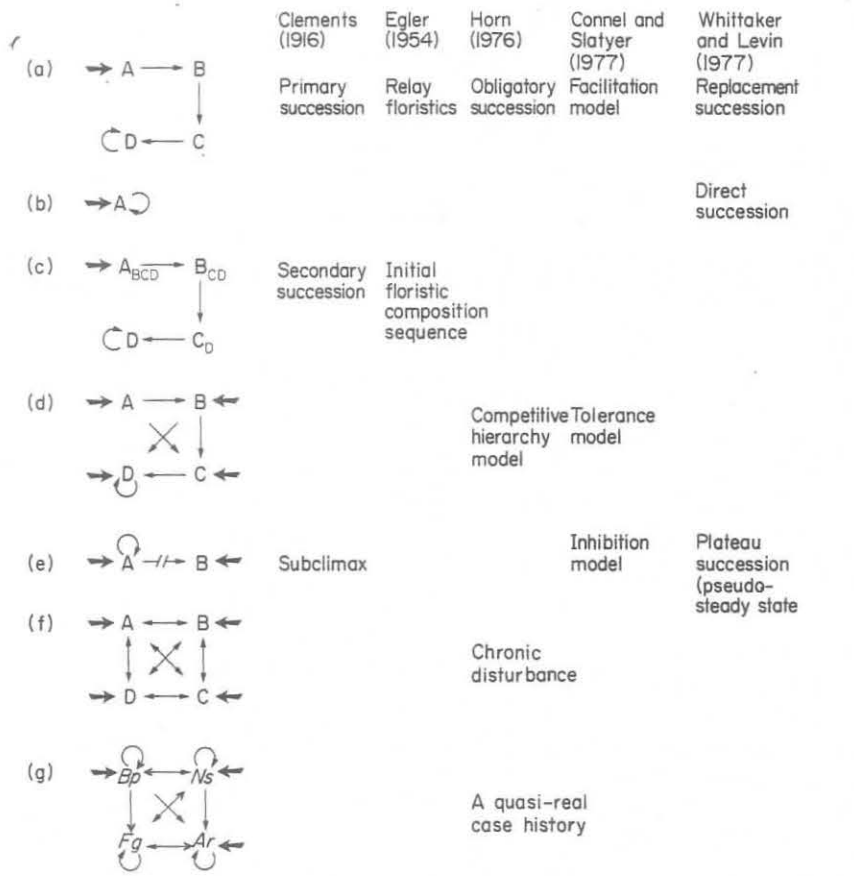

FIG. 1.5. Replacement sequences in succession proposed by different authors. The letters A–D in (a)–(f) represent hypothetical vegetation types or dominant species; subscript letters in (c) indicate that species are present as minor components or as propagules—for simplicity, they have been omitted from (d)–(g); thin arrows represent species or vegetation sequences in time; bold arrows represent alternative starting points for succession after disturbance; in (g), *Bp*, *Ns*, *Ar* and *Fg* represent *Betula populifera*, *Nyssa sylvatica*, *Acer rubrum* and *Fagus grandifolia* respectively, and the three open-headed arrows represent less frequent transitions. (After Noble 1981.)

can invade, Connel & Slatyer (1977) called this the 'tolerance' model. The 'tolerance' model certainly operates to some extent during primary succession, but as the soil at the beginning of secondary succession is never without propagules of some species, it will never occur then without an element of the initial floristic composition model.

Fig. 1.5e depicts what happens when a stand of vegetation somehow

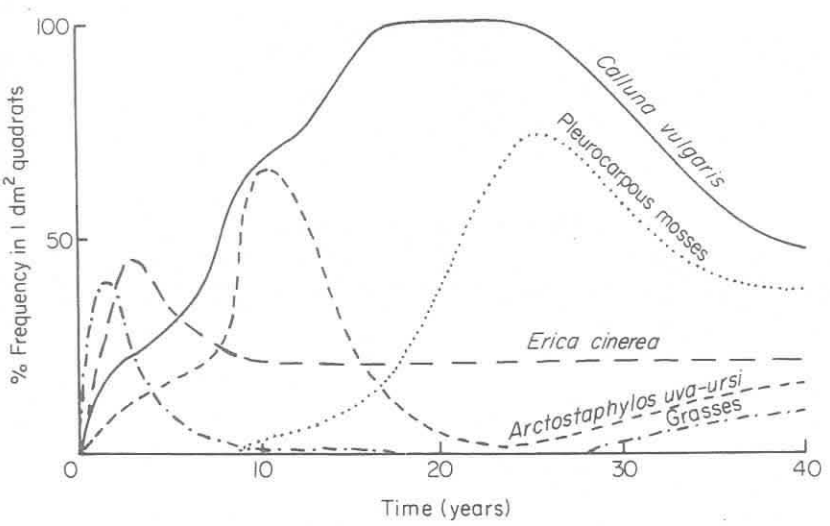

FIG. 1.6. Generalized sequence of vegetation change after fire on Dinnet Moor, north-east Scotland. (After Hobbs, Mallik & Gimingham 1984.)

'resists' invasion by plants of higher life-form. Connel & Slatyer called this 'inhibition'; Whittaker & Levin (1977) termed it 'plateau succession' in reference to the persistence of a non-climax stage. Clements (1916) called any vegetation prevented, temporarily or permanently, from developing into climax vegetation, 'subclimax', and noted that subclimax could be caused by competition.

Horn (1976) suggested that chronic, patchy disturbance could give a situation where any species could, if propagules were present, invade an opening resulting from the death of any other species (Fig. 1.5f). Clearly such a mechanism could operate at the level of individual plants or small patches. It is likely that such purely probabilistic succession never occurs as the sole mechanism in any stand, but Horn suggests that some of the celebrated local diversity of tropical forests could be due to this mechanism.

It seems clear that no succession, primary or secondary, ever occurs in which any single one of these models operates alone. Fig. 1.7 gives the generalized sequence of vegetation change when *Betula pendula* or *B. pubescens* colonizes *Calluna*-dominated moorland in the Scottish Highlands. The early changes follow the 'initial floristic composition' sequence. *Calluna* cannot regenerate vegetatively under a developing *Betula* canopy, and as it dies of old age it is replaced by species that can spread

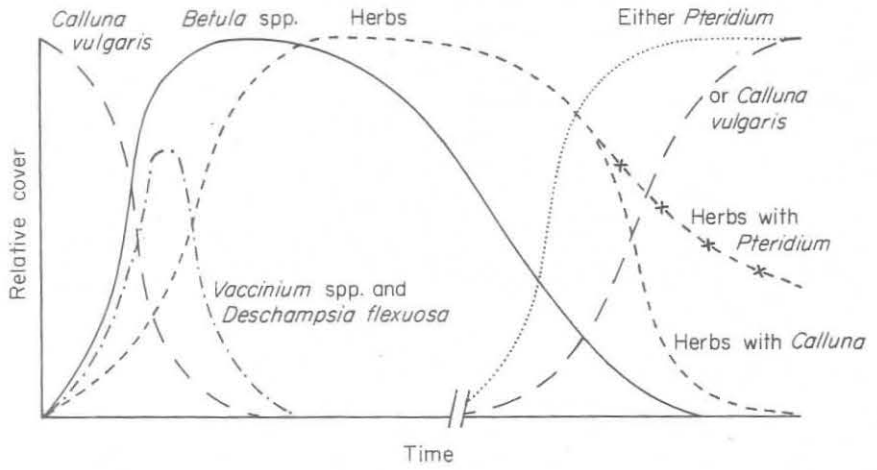

FIG. 1.7. Generalized sequence of vegetation change during the life-cycle of a Scottish Highland birchwood. (After Miles 1981b.)

by vegetative means; variously *Deschampsia flexuosa*, *Vaccinium myrtillus* and *V. vitis-idaea*. A dense substratum of pleurocarpous mosses also forms. Experimental sowings have shown that the field layer then prevents establishment of woodland herbs that can otherwise grow in that soil; this is 'inhibition'. Eventually, however, herbs characteristic of woodland and grassland do invade, spread, and except at sites with very poor soils, largely suppress the earlier dominants. The mechanisms by which this occurs are still unclear, but this changeover always parallels soil changes tending to produce brown podzolic profiles in place of podzols. Many of these later colonizers cannot grow, even without competition, in the moorland soils, so the soil changes resulting from the earlier vegetation changes 'facilitate' this phase of the succession, which itself probably operates along the lines of the 'tolerance' model. Finally, as the *Betula* stand dies of old age, *Calluna* begins to re-establish, probably mainly from seed blown in, though small quantities of seed can still occur in the soil seed bank after 90 years. However, if small amounts of *Pteridium aquilinum* are present, they are likely to develop into a dense stand after the release from shading; or if a *Pteridium* stand occurs close by, it can then invade. Either way, a dense stand of *Pteridium* can develop which prevents *Calluna* re-establishment. Seeds or fruits of later successional trees (e.g. *Pinus sylvestris*, *Quercus petraea*) are rarely present, because of the extent of past deforestation. The main sequence of change thus

occurs according to, or compatibly with, the sequence of models: initial floristic composition, inhibition, facilitation and tolerance, initial floristic composition or inhibition.

Horn (1976) estimated transition probabilities of tree species in a New Jersey forest formed on abandoned farmland. The inferred replacement series is shown in Fig. 1.5g. He noted that the overall pattern was of a competitive hierarchy (tolerance model), with chronic, patchy disturbance also involved, and 'a hint' of obligatory succession (since *Fagus grandifolia* rarely invades open fields there), plus some self-replacement (i.e. direct succession).

In sum, the models in Fig. 1.5 relate to the succession of particular species in particular situations, and not to vegetation types. This is an unsurprising conclusion, because in succession it is individuals and populations that change. For vegetation to act in successional terms as a unit, and thus to permit useful generalizations about succession at a vegetation level, it would need to be a tightly integrated network of species, probably co-evolved and co-adapted, possessing hypothetical 'emergent' properties, and thus behaving as a vegetational gestalt. There is negligible evidence to support such a view. No properties of vegetation have ever been demonstrated that cannot be explained as the effects of species and of interactions between species. In contrast, much evidence supports Gleason's (1926, 1937) view of the probabilistic nature of vegetation, which predicts that no two patches of vegetation are ever likely to be identical in composition, except by chance. Perusal of the relevés in phytosociological publications supports this idea. Further, the palynological record of invasions and interglacial plant successions, e.g. Fig. 1.8, confirms that vegetation types are not persistent in time, so are unlikely ever to develop the level of integration needed to behave as a unit (West 1964; Watts 1973; Davis, Chapter 18). To quote West (1964): '... we may conclude that our present plant communities have no long history in the Quaternary, but are merely temporary aggregations under given conditions of climate, other environmental factors, and historical factors.'

CURRENT ATTITUDES TO SUCCESSION

I am not aware of any current consensus view about succession, but I shall state what I believe to be the prevalent attitude. Only a tiny proportion of the earth's surface is currently undergoing primary succession as defined by Clements (1916) (although, because the Quaternary climate is never stable, primary succession in theory never ends). Understanding of primary successions has practical use in the reclamation of

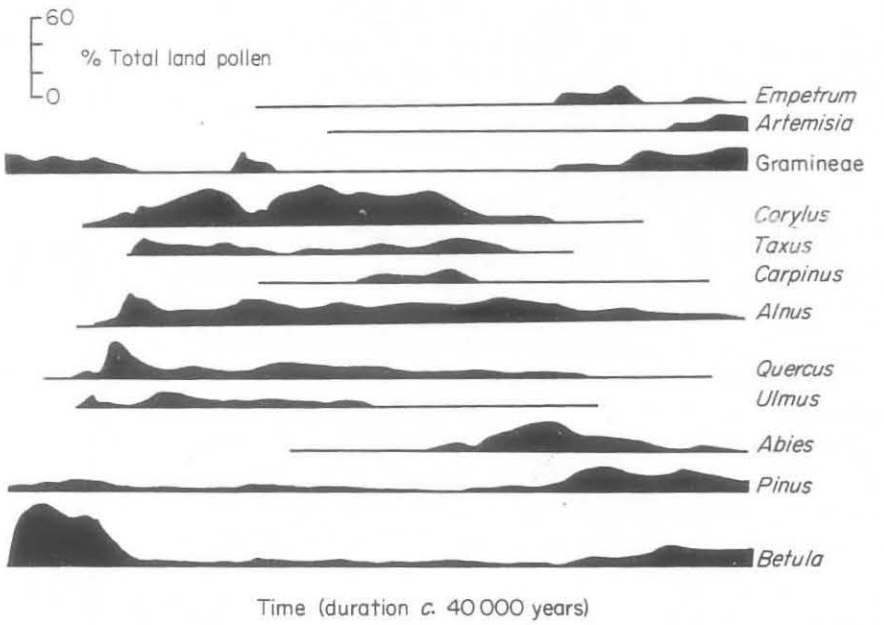

FIG. 1.8. Vegetation changes at Marks Tey, Essex, during the Hoxnian interglacial period. (From Turner 1970, courtesy of the Royal Society.)

quarry spoil and industrial wastelands, while understanding of secondary successions is of direct concern to vegetation managers, farmers and foresters. Hopefully, the quest for unifying, generalized theories of succession has been abandoned. Certainly there is now concentration on three topics: mechanisms of succession, modelling and predicting succession, and understanding the processes that determine the structure and species composition of vegetation.

The first topic, mechanisms of succession, is still poorly understood. More data are needed to test the current speculations and hypotheses, and to develop new hypotheses. This partly accounts for the recent proliferation of studies in permanent plots in continental Europe (Maarel 1984), and it is to be hoped that this may do for vegetation dynamics what the continental Europeans earlier did for static, descriptive vegetation science. There is interest in pursuing the use of 'vital attributes' (Noble & Slatyer 1977, 1979, 1980), but these need to be linked with quantitative methods of predicting change, and to allow for probabilistic events.

Modelling succession continues as a development point. There is a need to be able to model vegetation change as a tool in the use, management and sustaining of biological resources. Particular emphasis has been

given to modelling forest succession (Shugart, West & Emanuel 1981; Shugart 1984) because of the economic importance of forests, and because much is known about the life history and behaviour of many common tree species. Markov models have been used increasingly, despite their many limitations and imperfect assumptions (see Usher, Chapter 2). However, their extreme simplicity makes the underlying assumptions crystal clear, an advantage when computers allow the development of increasingly complex models which only a few people may really understand. The use of Markov models can be a useful way of examining largely unknown systems (Miles *et al.* 1985).

Third, there is a valuable concentration on examining the mechanisms determining the structure and species composition of vegetation (Grubb 1977, 1984; Grime 1977, 1979, Chapter 20; Harper 1977; Hubbell 1979; Hubbell & Foster, Chapter 19). This is of crucial importance, because when these mechanisms are modified, by 'natural' events or by management, change in vegetation composition ensues. Equally they can explain how change can, or cannot, occur when new species attempt to invade.

AN EMPIRICAL APPROACH TO SUCCESSION

One aim of succession research should be to predict change in vegetation when or if management alters. Prediction can never be exact or in fine detail. However, predictions that are probabilistic and less detailed are in very many instances all that are needed. Prediction should ideally be made from an understanding of how any particular system functions. Acquiring such knowledge is a long process, and the need for management advice and prediction does not disappear in the meantime. Hence, there is a need for empirical, correlative studies to be pursued concurrently. With time, management advice should steadily improve by a process of successive approximation.

My main interest is in the use and management of semi-natural vegetation in the British uplands, and of similar vegetation in the lowlands. Nine years ago, I reviewed the scanty literature on change in such vegetation, and on its causes, chiefly grazing and fire. This was incorporated into a series of successional diagrams (Miles, Welch & Chapman 1978) which included estimates of rates of change at particular grazing pressures by sheep. These word models were then used to predict the changes in vegetation on part of Dartmoor, in south-west England, that might occur in 25 years given (i) an end to burning, and of grazing by domestic livestock, (ii) a burning frequency and grazing intensity as high as the vegetation could support (Fig. 1.9). If the rules used were formalized,

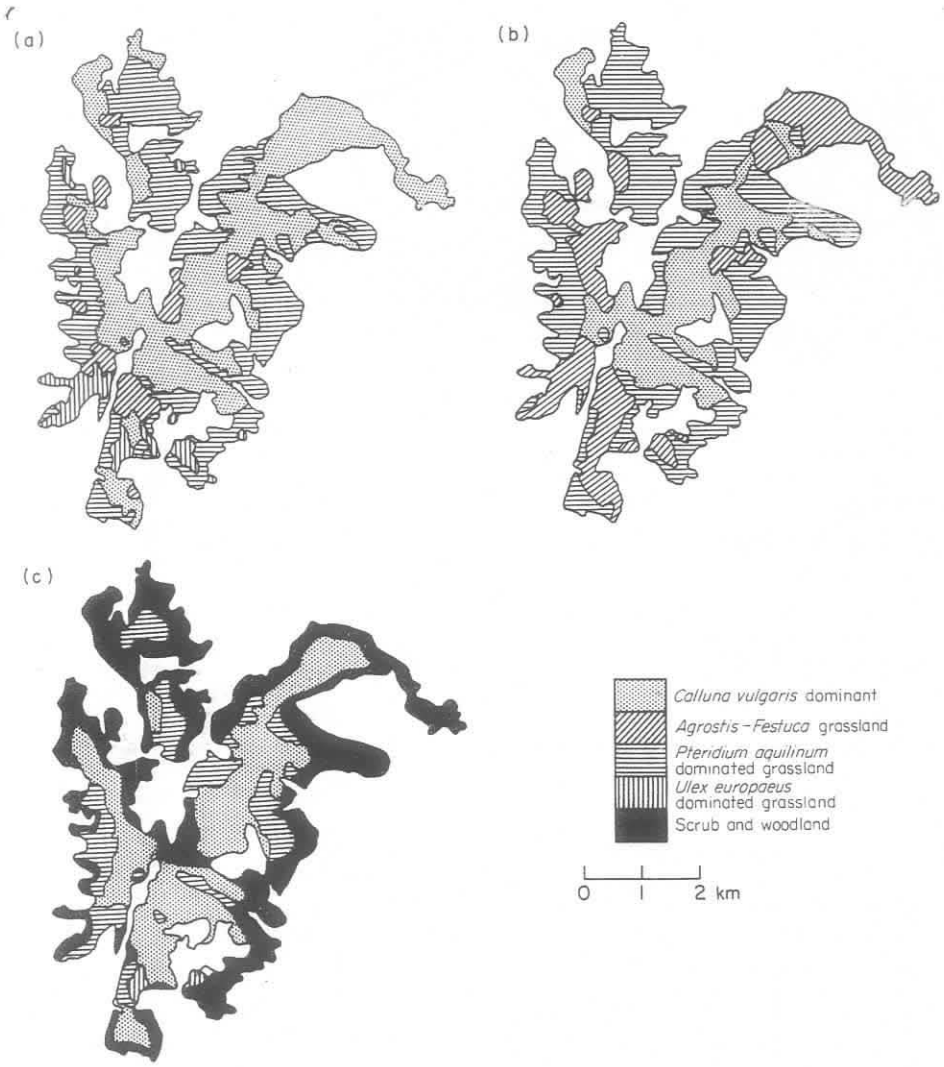

FIG. 1.9. Patterns of vegetation on well-drained soils of the Haytor moorlands, Dartmoor, south-west England: (a) as recorded in 1976; (b) predicted for 2001 if grazing by domestic livestock and burning were at the maximum that could be supported by the vegetation; (c) predicted for 2001 if grazing and burning cease. (From Miles, Welch & Chapman 1978, courtesy of the Countryside Commission.)

such an exercise could be done by an 'expert system' model. The main disadvantages were the hypothetical nature of some of the information used, and the impossibility of making probabilistic predictions.

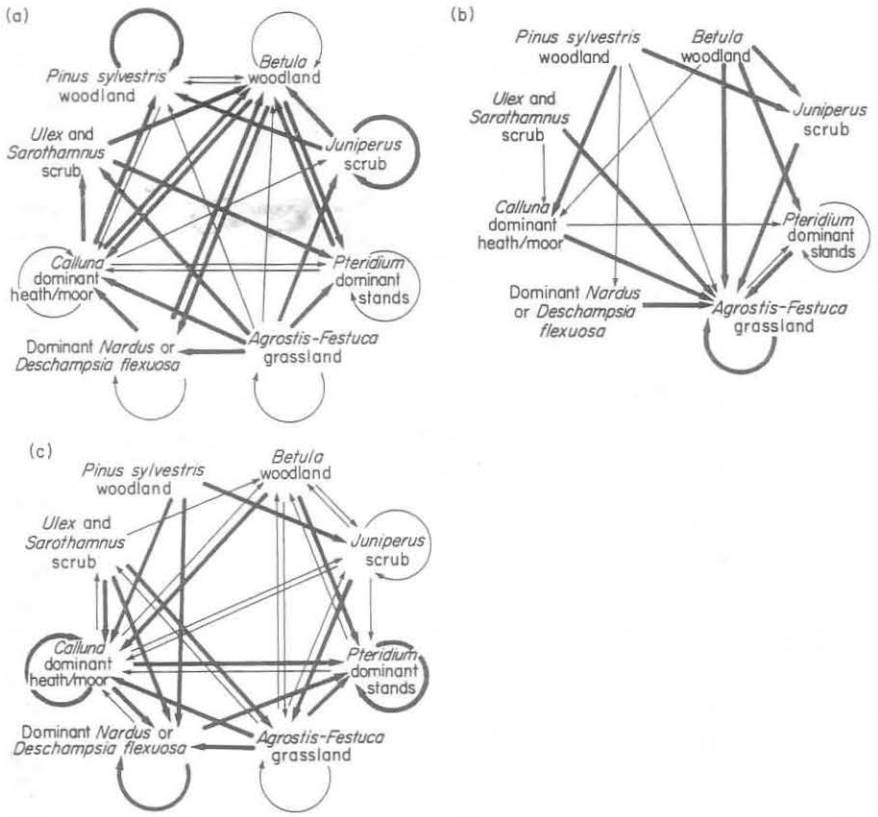

FIG. 1.10. Successional transitions in the British uplands (particularly north-west Scotland) between eight vegetation types given (a) low grazing pressures (<1 sheep equivalent ha^{-1} $year^{-1}$) and no burning, (b) high grazing pressures (>2–3 sheep equivalents ha^{-1} $year^{-1}$) and frequent burning, and (c) intermediate levels of grazing (1–2 sheep ha^{-1} $year^{-1}$) and occasional burning. Broad arrows represent common transitions, thin arrows less frequent transitions, and curved arrows self-replacement. The vegetation types are arranged so that types tending to podzolize and/or acidify soils are on the left, and types with contrasting pedogenic effects are on the right. (From Miles 1985b, courtesy of the British Society of Soil Science.)

We are now trying to collect the data needed to improve such predictions of succession, currently by the analysis of archival aerial photography in north-east Scotland. Formally, the exercise is structured to test the 1978 successional diagrams. Transitions that are known to occur at least sometimes, between various vegetation types on well-drained, mineral soils, and with high, medium and low intensities of grazing and burning, are shown in Fig. 1.10. The problem of species as against vegetation

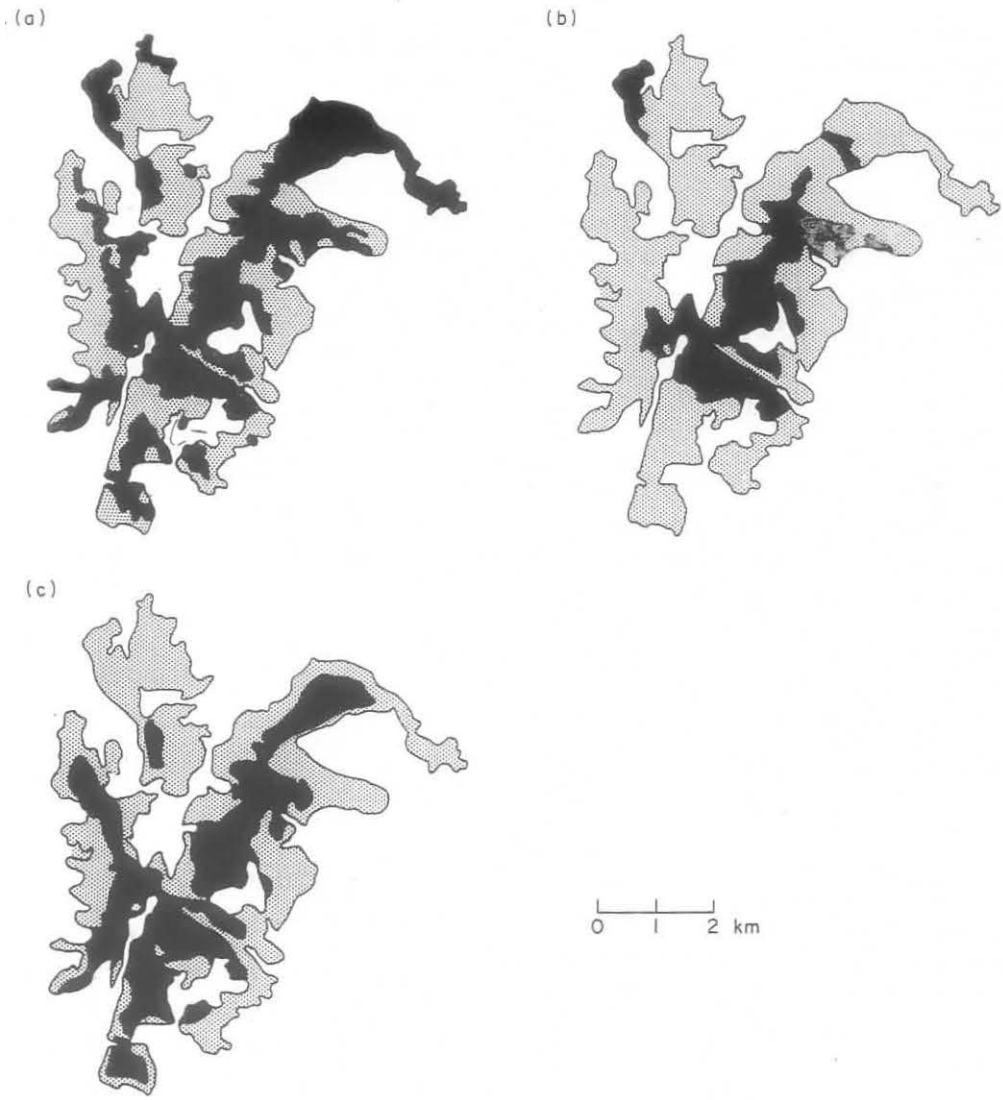

FIG. 1.11. Patterns of vegetation tending to podzolize and/or acidify soils (solid areas), and of vegetation with contrasting pedogenic effects (stippled areas), on well-drained soils of the Haytor moorlands, Dartmoor, south-west England: (a) as recorded in 1976; (b) predicted for 2001 if grazing by domestic livestock and burning were at the maximum that could be supported by the vegetation; (c) predicted for 2001 if grazing and burning ceased.

succession, discussed earlier, is overcome by using a physiognomic classification based on dominance. We believe this is sensible because dominant species *inter alia* give landscapes their characteristic colour and texture, have the greatest ecological effect, especially on the soil (Miles 1985b), and are the main resource for game, domestic livestock, and animals of nature conservation interest. Fig. 1.10 indicates that multiple pathways occur, but the extent to which they occur at a site or local level, or on a larger scale is not yet known. Equally there is little knowledge of variations in rates of change.

Fig. 1.10 is arranged so that species and vegetation known to podzolize or acidify soil are on the left, and those with contrasting tendencies on the right. Inclusion of pedogenic trends permits a new level of prediction. Even without a knowledge of the relative frequencies of the different transitions, inspection of Fig. 1.10a suggests that several vegetation types will tend to coexist within a catchment or landscape (albeit that forest may predominate): effectively the concept of multiple stable points (Sutherland 1974) or of the shifting-mosaic steady state (Bormann & Likens 1979). This would also give a mosaic of contrasting pedogenic trends which, because the mosaic pattern would change with time, might tend to cancel out and give effective equilibrium of soil properties at this scale. Fig. 1.10b suggests a dominant trend away from podzolization, towards brown podzolic soil/brown earth development. Fig. 1.10c suggests even more strongly than Fig. 1.10a that a mosaic of vegetation types and pedogenic trends would exist. Application of pedogenic trends to Fig. 1.9 gives Fig. 1.11. A mosaic effect is seen, shifting as management changes.

In sum, our empirical perspective of succession views a catchment or landscape as a mosaic of sites or ecotesseras (Jenny 1980). This gives the possibility of combining the probabilistic information on ecotesseras (at any scale) with a wider spatial perspective. Thus, we aim to use our knowledge of succession to predict vegetation change both probabilistically and cartographically. It should also be possible to integrate other information (e.g. models predicting element output and changes in faunal populations with changing vegetation) in such landscape-scale models. Seeking to apply ecological knowledge in this way will, on the one hand, expose its deficiencies, and on the other hand may, even if only partly successful, show the practical relevance of such knowledge, and thereby generate continued support for the subject.

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